

MORPHOLOGICAL AND REPRODUCTIVE
CHARACTERISTICS OF *LINANTHUS JEPSONII*
(POLEMONIACEAE), A NEWLY DESCRIBED,
GEOGRAPHICALLY RESTRICTED SPECIES FROM
NORTHERN CALIFORNIA

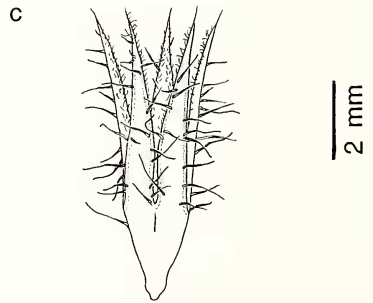
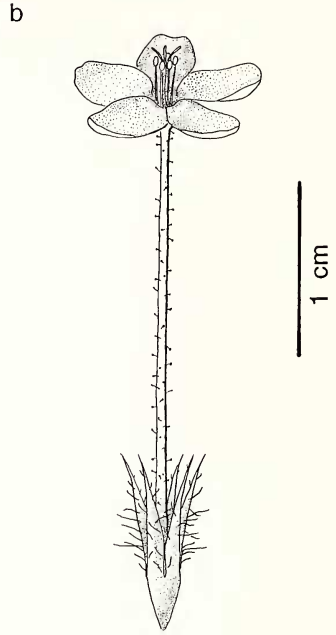
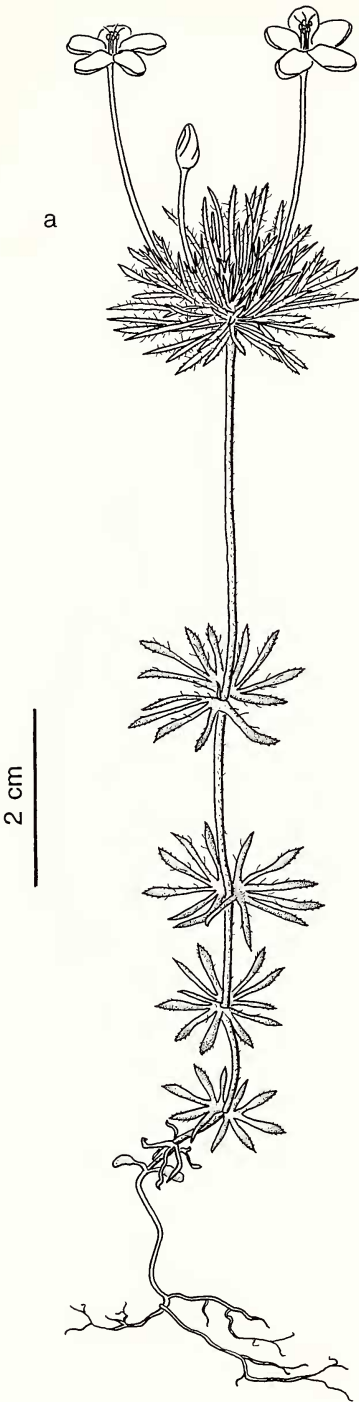
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ABSTRACT

Linanthus jepsonii is a newly described species in the *L. androsaceus* complex (sect. *Leptosiphon*) restricted to Lake, Napa and Sonoma Cos. in the California North Coast Range. Multivariate analyses of six morphological characters revealed that *L. jepsonii* is readily distinguished from the other species in the complex found in the same region. It is ecologically and morphologically most similar to *L. parviflorus*, but can be distinguished from this species by its long calyx, the long, sparse hairs on the calyx lobes and its self-compatible breeding system. Greenhouse experiments indicate that these taxa are reproductively isolated, as crosses between them produce few seeds, and hybrid plants are typically male sterile.

Field and laboratory studies to examine the evolution of a flower color polymorphism in the California annual *Linanthus parviflorus* (Benth.) Greene led to the discovery of a new species in the *Linanthus androsaceus* complex [*L. androsaceus* (Benth.) Greene, *L. parviflorus* (Benth.) Greene, *L. latisectus* Buxton, *L. bicolor* (Nutt.) Greene, *L. acicularis* Greene, and *L. serrulatus* Greene], sect. *Leptosiphon* (Endl.) V. E. Grant (Grant 1959). The new species is superficially very similar to *L. parviflorus*, and can be found in similar habitats, but differs from it in breeding system and in several distinctive morphological characters, most notably calyx pubescence. Crosses between the new species and *L. parviflorus* produce few seeds, and the few hybrids that survive are typically sterile. The morphological and reproductive characteristics of the new taxon are sufficiently distinct from other members of the section *Leptosiphon* to warrant species status. Field observations and an extensive survey of herbarium specimens indicate that the new species has a restricted geographic range, being found only in Lake, Napa and Sonoma Cos. We have chosen to name this species in honor of the renowned botanist Willis Linn Jepson, who collected the first specimen in 1893, one hundred years before publication of *The Jepson Manual* (Hickman 1993).

Linanthus jepsonii D. W. Schemske and C. Goodwillie, sp. nov.
(Fig. 1). —TYPE: USA, California, Napa County, Wantrup Wild-



life Sanctuary, on primary road 1.3 km W of Hardin Rd., and 60 m N of vernal pool on north-facing, grassy slope, elev. 256 m, 11 May 1995, *C. Goodwillie* 001 (holotype WTU; isotypes CAS, JEPS, MO, RSA, SFSU and US).

Caules erecti; raro ramosi, 4–12 cm alti; folia recta, sursum angulata, lobo medio lineari, 0.8–1.1 mm lato; calyx 6–9 mm longus, apicibus recurvis, superficie adaxiali calicis marginibusque sparse villosis, trichomatibus mollibus, 0.7–1.6 mm longis; corollae tubus 20–36 mm longus, rubellus; corollae lobi 4–6 mm, ovales, angulis rectis tubo conjuncti, sursum concavuli, rubelli vel albi; stigmata 0.8–2.0 mm longa, clavata, plerumque excedentia antheras easque superantes; inflorescentia pauci vel multiflora, floris 1–2 (3) uno tempore florentibus.

Annual. Stems erect, green or rose, pubescent, rarely branched, 4–12 cm high. Leaves opposite, straight, angled upwards, palmately divided; leaves subtending inflorescence 5–8 lobed, middle lobe linear, 0.8–1.1 mm wide, 8–13 mm long, lateral lobes similar, adaxial surface and margins sparsely villous, trichomes 1–1.5 mm long, abaxial surface glabrous; lower leaves 3–8 lobed, middle lobe linear to spatulate, lateral lobes less spatulate, trichomes shorter and less dense than on upper leaves. Inflorescence head-like, terminal, typically one per plant, 1–2 (3) flowers open at a time, 4–15 flowers per inflorescence, flowers sessile; calyx 6–9 mm long, 5-lobed with a membrane half the width of calyx lobe, tips recurved, adaxial surface and margins of calyx lobe sparsely villous, trichomes 0.7–1.6 mm long, abaxial surface glabrous. Corolla salverform; tube 20–36 mm long, 0.6 mm in diameter, glabrous to sparsely puberulent, glandular, pink; throat yellow; lobes 4–6 mm long, oval, at right angles to tube, somewhat concave upwards, pink or white. Stamens exerted, filaments 2 mm long. Style thread-like, exerted; stigmas 0.8–2.0 mm long, clavate, yellow, generally overlapping with and extending somewhat beyond anthers. Capsule obovoid with 3 locules, up to 6 seeds per locule, dehiscent. Seeds 1.2 mm long, angular, corrugated, yellowish-tan, mucilaginous when wet.

Paratypes. USA, California: Lake Co., Mt. St. Helena, 30 Apr 1933, *Mason 7217* (UC); Collayomi Valley, 19 Apr 1936, *Jepson 17417* (JEPS); Napa Co., Calistoga, 2 May 1893, *Jepson s.n.* (JEPS, UC); Pope Valley, 15 May 1920, *Ferguson 349* (JEPS, MO); Conn

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FIG. 1. *Linanthus jepsonii* D. Schemske and C. Goodwillie. **a**, habit illustrating unbranched stem, few-flowered inflorescence and long corolla tubes. **b**, calyx and corolla, with stigma lobes overlapping the anthers. **c**, calyx with recurved tips and long hairs sparsely distributed on the adaxial surface of the calyx lobes.

Valley, Napa Range, 6 Apr 1924, *Jepson 10315* (JEPS); Mt. St. Helena, 2 mi below Patten's, 21 Mar 1926, *Howell 1735* (CAS); St. Helena Grade, 3 May 1928, *Abrams 12220, 12221* (DS); 2 mi S of Hawkins Mtn. Inn Camp, 3 May 1928, *Wolf 1792* (DS); 1.5 mi W of Yountville, 22 Apr 1938, *Constance 2135* (MO, UC); Dry Creek Rd., 28 May 1960, *Ruckert 164* (CAS); Hwy. 29, 8 Apr 1971, *Shevock 920* (CAS); Sonoma Co., Cagadero, 2 May 1926, *Bacigalupi 1366* (DS); hillside opposite Maple Glen, 7 May 1927, *Baker 21441* (UC); Reibli School near springs, 13 Apr 1928, *Mason 4339* (UC); Santa Rosa, 24 Apr 1931, *Eastwood 10365* (CAS); near Mark West Springs, 15 May 1938, *Eastwood and Howell 5508* (CAS); 15 mi from Geysers, Sulfur Creek Canyon, 22 Apr 1940, *Koch 832* (UC); head of Maycama Creek, Knights Valley, 21 May 1940, *Mason 12293* (UC); vicinity of Bechtel Cabin, Pepperwood, 30 Mar 1981, *Almeda and DeNevers 4878* (CAS); Pippindale Farm, Hansel's cow pasture, Pepperwood, 8 Apr 1981, *DeNevers 664* (CAS); 4.5 mi NE of Pengrove on W slope of Sonoma Mtn., 14 May 1981, *Howell et al. 53956* (CAS); grazed shore of Hansel's cow pasture, Pepperwood, 15 May 1981, *DeNevers 1205* (CAS); Pepperwood Ranch W of Knights Valley, 11 Apr 1983, *Breedlove 58684* (CAS); 2 mi NE of Bechtel Cabin, Pepperwood, 1 May 1993, *de Geofroy 036* (SFSU).

Distribution. *Linanthus jepsonii* has a restricted distribution in the California North Coast Range, occurring only in Lake, Napa and eastern Sonoma Cos., at elevations from 200–500 m. In a sample of 2402 herbarium specimens that had been classified as *L. parviflorus*, *L. bicolor*, or *L. androsaceus* (from CAS, DS, JEPS, MO, RSA, SFSU and UC), we found only 35 that could be assigned to *L. jepsonii*, all occurring in Lake, Napa and Sonoma Cos. Extant populations were observed in Napa Co. (four populations) and Sonoma Co. (one population).

Habitat, life history and reproductive biology. *Linanthus jepsonii* is found on open or partially-shaded, grassy slopes, principally on volcanic soils, and occasionally on the periphery of serpentine soils. The seeds of *L. jepsonii* germinate during winter rains, and flowering occurs from early April through May. Fruits mature in 3 weeks, and seeds are dispersed by explosive dehiscence of the capsule. Although *L. jepsonii* is variable for flower color (pink or white corolla lobes), pink-flowered plants predominate (>95% of all plants) in three of the five populations of *L. jepsonii* we have observed, and white-flowered plants predominate in the other two populations. Despite its restricted geographic range, *L. jepsonii* often forms dense populations, with population sizes ranging from 400 to >>10,000.

Linanthus jepsonii is visited and pollinated by beeﬂies (*Bombylius*

spp.), but is fully self-compatible and capable of autogamy, as indicated by greenhouse experiments that found no significant difference in seed set in hand self-pollinations (mean = 8.7, n = 88), cross-pollinations (mean = 8.4, n = 87), and unmanipulated flowers (mean = 8.0, n = 89).

SPECIES RELATIONSHIPS

The floral characters of *L. jepsonii* place it in the section *Leptosiphon*, a group of annual *Linanthus* species first recognized by Grant (1959) and characterized by sessile flowers borne in terminal heads, with filiform tubes much exerted beyond the calyx (Buxton 1994). Although we have not made a chromosome count, electrophoretic data gathered for mating system estimation (Goodwillie and Schemske, unpublished) suggest that *L. jepsonii* is diploid, as are all other species in this section for which cytological information is known (Patterson 1979, 1993).

Morphology. Flower and calyx size, and calyx pubescence have been widely used in taxonomic treatments of the Polemoniaceae (Patterson 1993, Buxton 1994, Gordon-Reedy 1990). To compare the morphology of *L. jepsonii* to other members of the *Linanthus androsaceus* complex (sect. *Leptosiphon*) found in the same region, we measured the length of the corolla lobe, corolla tube, stigma, calyx, and calyx hairs, and counted the number of hairs on the calyx of 30 individuals for each of five populations of *L. jepsonii* (from Lake, Napa and Sonoma Cos.) and *L. parviflorus* (from Lake, Napa and Sonoma Cos.), and for each of two populations of *L. androsaceus* (from Napa County), *L. bicolor* (from Napa County) and *L. latisectus* (from Mendocino and Sonoma Cos.). The total sample comprised 480 individuals from 10 different localities. Figure 2 presents the mean value for each of the six characters for the four species examined, and provides a statistical analysis for those pairwise comparisons to *L. jepsonii*. To determine if the mean value of a character in *L. jepsonii* was significantly different from that in each of the other species, we conducted an analysis of variance (ANOVA; SAS Institute 1994) for each of the four pairwise combinations involving *L. jepsonii*, with population nested within species. Significance levels were adjusted for multiple comparisons of each character following the procedure of Rice (1989). *L. bicolor* was found to differ significantly from *L. jepsonii* for each of the six characters, and *L. latisectus* was significantly different from *L. jepsonii* for all characters except stigma length. *L. androsaceus* was significantly different from *L. jepsonii* for corolla lobe length, corolla tube length, stigma length, and calyx length, and *L. parviflorus* was significantly different from *L. jepsonii* for stigma length, number of calyx hairs, calyx hair length and calyx length (Fig. 2).

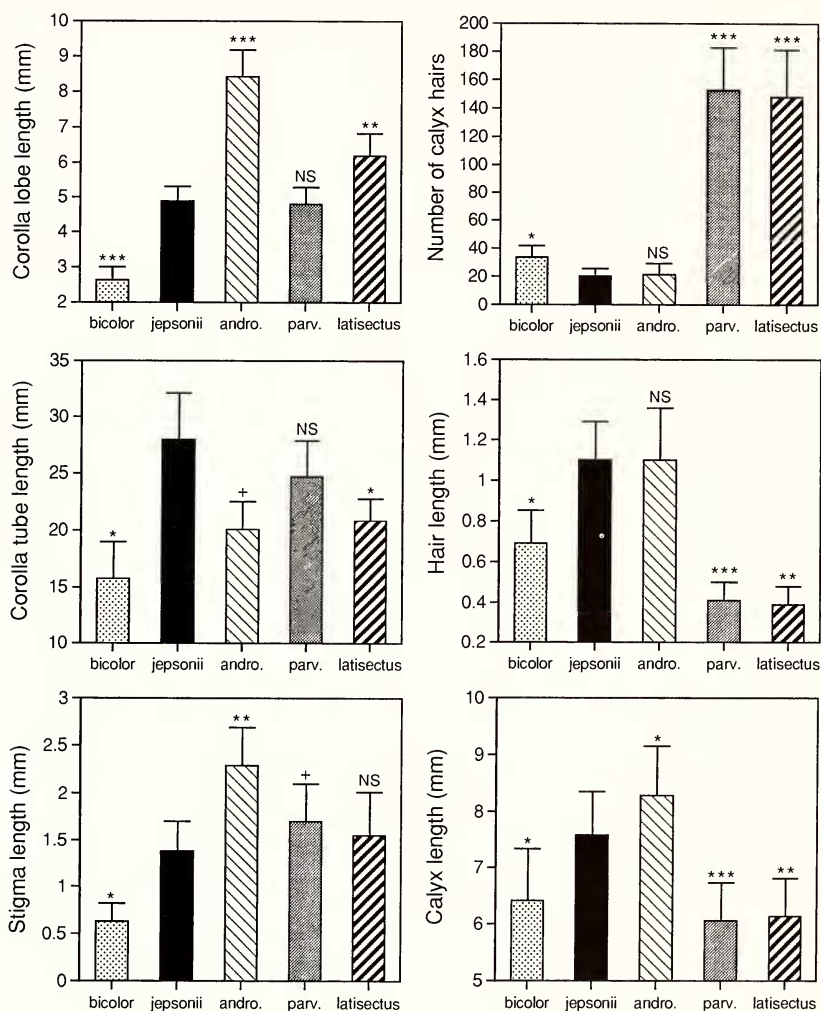


FIG. 2. Comparison of reproductive characters for five species in the *Linanthus androsaceus* complex, section *Leptosiphon*. Means and 2 SE are presented, based on a sample of 30 individuals for five populations of *L. jepsonii* and *L. parviflorus*, and two populations of *L. androsaceus*, *L. bicolor* and *L. latisectus*. The number of calyx hairs was determined for the adaxial surface of one calyx lobe (including lobe margins), and hair length represents the mean of the longest two hairs on one calyx lobe. The symbols over the bars indicate if a given species was significantly different from *L. jepsonii*; + $P < 0.06$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant.

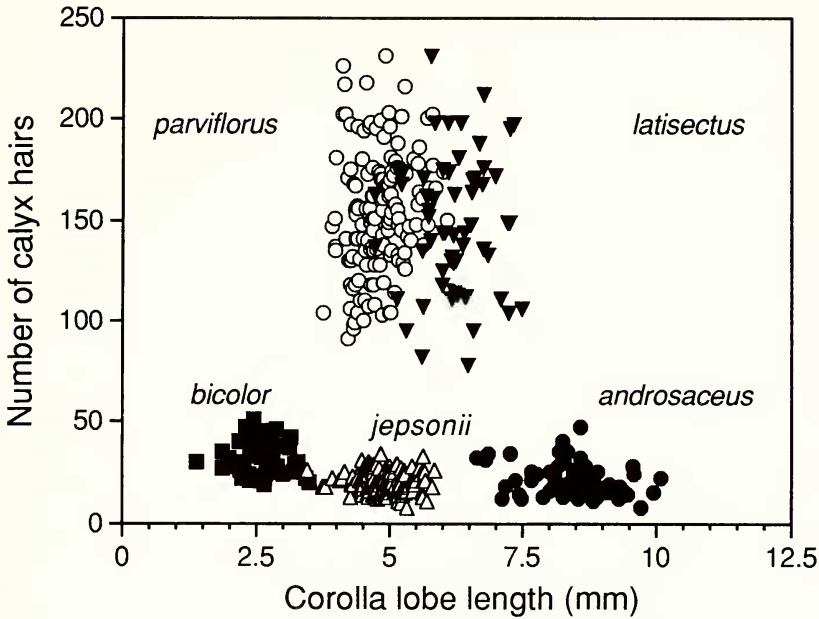


FIG. 3. Scatter plot for the number of hairs on the adaxial surface of one calyx lobe (including lobe margins) and corolla lobe length for specimens of five species of *Linanthus*. Numbers of individuals and populations are given in Figure 2.

A multivariate analysis of variance (MANOVA; SAS Institute 1994) conducted on all six characters indicated highly significant differences among species (Wilks' Lambda = 0.0016, $F = 361$, $df = 24/1641$, $P < 0.0001$). A discriminant analysis (SAS Institute 1994) was then used to determine how accurately the six characters, taken together, would classify the specimens into their correct taxon. The discriminant analysis was highly significant (Likelihood ratio = 695.6, $X^2 = 1391$, $P < 0.0001$, $R^2 = 0.96$), correctly classifying 99% of the 480 specimens, including 149 of the 150 specimens of *L. jepsonii*. A discriminant function analysis conducted with corolla lobe length and the number of hairs on the calyx lobe was the best two-character model (as judged from classification accuracy), correctly classifying 96% of all specimens, and was as efficient as the full six-character model in classifying specimens of *L. jepsonii* (MANOVA: Wilks' Lambda = 0.00997, $F = 1068$, $df = 8/948$, $P < 0.0001$; Discriminant Function Analysis: Likelihood ratio = 648.9, $X^2 = 1298$, $P < 0.0001$). A scatter plot of these two characters for all measured specimens is given in Figure 3. The number of calyx hairs divides the five species into two groups, one with many hairs, including *L. parviflorus* and *L. latisectus*, and the other

with few hairs, including *L. bicolor*, *L. jepsonii* and *L. androsaceus* (Fig. 3). In the group with sparse calyx pubescence, the corolla lobes of *L. jepsonii* are larger than those of *L. bicolor* and smaller than those of *L. androsaceus*, and the differences are sufficient to distinguish these species (Fig. 3).

Reproductive biology. In addition to the morphological characters discussed above, breeding system also varies considerably among species of the *L. androsaceus* complex. Although we do not have information on the reproductive biology of all species in the complex, our data are sufficient to make several comparisons of systematic significance. *L. bicolor* is self-compatible and appears to be highly selfing, as its diminutive flowers are rarely visited by pollinators (Goodwillie, personal observation). In contrast, both *L. jepsonii* and *L. parviflorus* are visited by bees (e.g., *Bombus* spp.), but they differ in breeding system. *L. parviflorus* is self-incompatible (Goodwillie in press), while *L. jepsonii* is self-compatible. In greenhouse experiments with *L. parviflorus*, seed set from hand self-pollinations was less than 5% of that from cross-pollinations, indicating the presence of a strong incompatibility system. Parallel experiments with *L. jepsonii* revealed no difference in seed number for selfed and outcrossed flowers. Mating system estimates were obtained from electrophoretic loci for populations of both species in Napa County. *L. parviflorus* was found to be 79% cross-pollinated, while *L. jepsonii* appears to have an intermediate mating system, with 43% of progeny derived from cross-pollination (Goodwillie and Schemske, unpublished).

Reproductive Isolation. An additional criterion for establishing the taxonomic rank of sympatric taxa is to determine the degree to which their populations are genetically isolated from one another. Sympatric populations that fail to produce fertile hybrids in the field are reproductively isolated, and therefore represent different biological species (Grant 1981; Mayr 1982).

Linanthus jepsonii overlaps the geographic distribution of four other species in the section *Leptosiphon*: *L. androsaceus*, *L. bicolor*, *L. latisectus*, and *L. parviflorus*. Preliminary genetic data based upon molecular markers suggest that *L. jepsonii* is most closely related to *L. bicolor* (Goodwillie, unpublished), but the high selfing rate of *L. bicolor*, and our observation that *L. bicolor* and *L. jepsonii* do not co-occur at the population level, suggest that these two species are reproductively isolated in the field. Our failure to find hybrids between these taxa supports this conclusion. Nor have we observed hybrids between *L. jepsonii* and *L. androsaceus* or *L. latisectus*. In contrast, we have observed several individuals that appear to be hybrids between *L. jepsonii* and *L. parviflorus* at two localities where these species have adjacent populations ("Litto Ranch" and "Mast Hill" in Napa County). Because *L. jepsonii* and *L. parviflorus* share the same polli-

nators, are either fully (*L. parviflorus*) or partially (*L. jepsonii*) outcrossing, and often grow in close proximity, interspecific pollen flow is more likely to occur between these two species than between *L. jepsonii* and other members of the *L. androsaceus* complex.

To assess the degree of reproductive isolation between *L. jepsonii* and *L. parviflorus*, we conducted inter- and intraspecific crosses in the greenhouse on plants grown from seeds collected from three sites with populations of both *L. jepsonii* and *L. parviflorus* (Litto Ranch and Mast Hill in Napa County, and Pepperwood Ranch in Sonoma County). All pairwise combinations of inter- and intraspecific crosses were conducted, both within and among sites (including reciprocals) with 3–5 plants crossed for each taxon and site. This resulted in 18 interspecific combinations (3 sites with a given species as the male parent \times 3 sites with the other species as the female parent \times 2 species/site = 18 combinations), and 9 different intraspecific combinations for both *L. jepsonii* and *L. parviflorus* (3 sites with a given species as the male parent \times 3 sites with the same species as the female parent = 9 intraspecific combinations for each species). We counted the number of filled seeds produced for each cross, and scored germination success and survival to flowering. The number of seeds planted for inter- and intraspecific crosses, respectively, was 490 and 683. In a second experiment we scored pollen fertility for inter- and intraspecific crosses conducted on the two species collected from the Litto Ranch site. We determined the percent of plants producing some pollen, and for a subset of these plants, we used lactophenol-aniline blue stain (Maneval 1936) to quantify the percent viable pollen (100 pollen grains from 20 plants of each cross type). We combined the data for intraspecific crosses of the two species, and made statistical comparisons of the intraspecific cross type to the interspecific cross type using a Mann-Whitney U-Test for seed number (18 combinations/cross type), germination (18 combinations/cross type), survival (18 combinations/cross type), and percent viable pollen ($n = 20$ plants/cross type), and a Fisher's Exact Test for the percent of plants with good pollen ($n = 56$ plants from intraspecific crosses; $n = 32$ plants from interspecific crosses). While this analysis is based on pollen viability data for only one locality, preliminary observations of the crosses for other localities gave similar results.

The results indicate strong barriers to gene flow between *L. jepsonii* and *L. parviflorus* (Table 1). For each of the characters examined, the performance of intraspecific crosses exceeded that of interspecific crosses, and these differences were significant in four of the five comparisons (Table 1). The greatest differences were observed for seed number and percent germination, for which intraspecific crosses outperformed interspecific crosses by approximately 2 fold, and percent viable pollen production, which was 13 fold

TABLE 1. SUMMARY OF THE PERFORMANCE OF INTERSPECIFIC AND INTRASPECIFIC CROSSES INVOLVING *LINANTHUS JEPSONII* AND *L. PARVIFLORUS*.

Performance criteria	Cross type		Prob. level
	Intraspecific	Interspecific	
Mean number of seeds per fruit	4.9	1.8	<0.0001
Mean % germination	63.7	32.4	<0.05
Mean % survival	61.6	40.5	0.15
% of plants with some good pollen	100.0	84.4	<0.01
% viable pollen in fertile plants	84.0	6.4	<0.0001

higher in intraspecific crosses. The low pollen viability of hybrids produced in the greenhouse is consistent with our observation that hybrids between these taxa in the field are generally male sterile. We conclude that *L. jepsonii* and *L. parviflorus* are reproductively isolated, and that they therefore satisfy the criterion of biological species as defined by Mayr (1982).

Classification. The discontinuities in morphological and reproductive characters observed between *L. jepsonii* and other sympatric *Linanthus* species, and its reproductive isolation from *L. parviflorus*, support recognition of *L. jepsonii* as a taxonomic species. To develop a classification for *L. jepsonii* and related taxa we revised the key provided by Patterson (1993) in The Jepson Manual (Hickman 1993), incorporating information on *L. latisectus* from Buxton (1993). In so doing, we were able to keep much of Patterson's classification, adding only those sections needed to distinguish *L. androsaceus*, *L. jepsonii*, *L. latisectus* and *L. parviflorus*. We use calyx pubescence as a major character for classifying these taxa, based on our finding that it consistently distinguished *L. parviflorus* and *L. latisectus* from *L. bicolor*, *L. jepsonii* and *L. androsaceus* in the 480 specimens analyzed in our survey (Fig. 3). Calyx pubescence may not be sufficient to distinguish these two groups in all localities, as evidenced by one population of *L. parviflorus* that has glabrous calyces and one population of *L. androsaceus* with short trichomes on the calyx (Buxton, personal communication), so in some cases it may be necessary to use other characters, such as those presented in Figure 2, or discussed by Patterson (1993) or Buxton (1993). The key below is intended to replace couplet 17 in Patterson (1993):

1. Calyx sparsely hairy on lobe margins, gen glabrous elsewhere, <50 total hairs on adaxial surface (including lobe margins); hairs >1 mm long
2. Corolla tube gen <25 mm long, lobes 7–10 mm long; NCoR, SnFrB
..... *L. androsaceus*
- 2' Corolla tube gen >25 mm long, lobes 4–6 mm long; NCoR . . . *L. jepsonii*
- 1' Calyx densely hairy throughout, >100 total hairs on adaxial surface (including lobe margins); hairs <0.5 mm long
3. Middle lobe of upper leaves 2–3.5 mm wide; corolla lobe gen >6 mm long; NCoR *L. latisectus*
- 3' Middle lobe of upper leaves <2 mm wide; corolla lobe gen <6 mm long; CA-FP *L. parviflorus*

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